

(19)



Europäisches Patentamt

European Patent Office

Office européen des brevets



(11)

EP 0 818 465 A1

(12)

EUROPEAN PATENT APPLICATION

(43) Date of publication:

14.01.1998 Bulletin 1998/03

(51) Int. Cl.⁶: **C07K 14/195**, **C12N 15/74**,
C12N 15/31

(21) Application number: **96730001.3**

(22) Date of filing: **12.07.1996**

(84) Designated Contracting States:

**AT BE CH DE DK ES FI FR GB GR IE IT LI LU MC
NL PT SE**

Designated Extension States:

AL LT LV SI

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listing and declared, that it includes no new matter.

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(54) **Genomic sequence of *Rhizobium* sp. NGR234 symbiotic plasmid**

(57) The sequencing and analysis of the complete nucleotide sequence of symbiotic plasmid pNGR234a isolated from *Rhizobium* sp. NGR234. The complete sequence of pNGR234a is presented. The analysis includes the identification of a number of novel ORFs and the proteins expressible therefrom which have been ascribed putative functions.

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BACKGROUND OF THE INVENTION

This invention relates to a symbiotic plasmid of the broad host-range *Rhizobium* sp. NGR234 and its use. In particular, this invention relates to the isolation and analysis of the complete sequence of the NGR234 symbiotic plasmid pNGR234a, and the open reading frames (ORFs) identifiable therein as well as the proteins expressible from said ORFs.

Together with carbon, hydrogen and oxygen, nitrogen is one of the essential components in organic chemistry. Although it is present in vast quantities in the atmosphere, nitrogen in its diatomic form N_2 remains unassimilable by living organisms. The nitrogen cycle begins by the fixation of nitrogen into ammonia which is chemically more reactive and can be assimilated into the food chain. A large fraction of the total nitrogen fixed every year is produced by micro-organisms. Among these, the soil bacteria of the genera *Azorhizobium*, *Bradyrhizobium*, *Sinorhizobium* and *Rhizobium*, generally referred to as rhizobia, fix nitrogen in symbiotic associations with many plants from the Leguminosae family. This highly specific interaction leads to the formation of specialized root-, and in the case of *Azorhizobium*, stem-structures called nodules. It is within these nodules that rhizobia differentiate into bacteroids capable of fixing atmospheric nitrogen into ammonia. In turn, ammonia diffuses into the vegetal cells and sustains plant growth even under limiting nitrogen conditions.

The *Rhizobium*-legume interaction presents many interesting features. Obviously, the possibility of using this symbiosis as an "environmentally friendly" way to provide some of the most important world crops (such as soybean, bean and many other legumes) with fixed nitrogen without using nitrate-rich fertilizers, has important economic consequence. It is also an ideal model to study a non-pathogenic interaction between bacteria and a highly developed, multicellular organism such as the host plant. Furthermore, the various steps involved in the establishment of a functional nitrogen symbiosis, which include some dramatic morphological changes as well as processes of cellular differentiation, require a complex exchange of molecular signals. Despite many decades of studies, it is only recently that the *Rhizobium*-legume interaction has been partially understood at the molecular level. The establishment of a functional symbiosis can be divided into two major steps as follows.

(A) Rhizosphere ecology and nodulation:

Rhizobia are soil bacteria that proliferate in the rhizosphere of compatible plants, taking advantage of the many compounds released by plant roots. In return it has been shown that the presence of rhizobia in the rhizosphere reduces susceptibility of plants to many root diseases. In the case of low nitrogen levels in the soil, compatible rhizobia can interact with host plants and start the nodulation process (Long, 1989; Fellay *et al.*, 1995; van Rhijn and Vanderleyden, 1995). Molecular signalling between the two partners begins with the release by the plant of phenolic compounds (mostly flavonoids) that induce the expression of nodulation genes (referred to as *nod*, *nol* and *noe* genes). The NodD1 gene product appears to be the central mediator between the plant signal and nodulation gene induction (Bender *et al.*, 1988). It is modified by the binding of flavonoids and acts as a positive regulator on the expression of the remaining nodulation genes. Among them, the *nodABC* loci encode products responsible for the synthesis of the core structure of lipooligosaccharides called Nod factors (Relić *et al.*, 1994). More nodulation genes are involved in strain-specific modifications of the Nod factors as well as in its secretion. It seems established now that variability in the structure of Nod factors may play a significant role in the determination of the host-range of a given *Rhizobium* strain, that is in its ability to efficiently nodulate different legumes. For example, the strain *Rhizobium meliloti* can only nodulate *Medicago*, *Melilotus* and *Trigonella* ssp., whereas *Rhizobium* sp. NGR234 can symbiotically interact with more than 105 different genera of plants, including the non-legume *Parasponia andersonii*.

The structure of many Nod factors, their isolation from *Rhizobium* strains and their commercial application in agriculture have been described (NodNGR-Faktoren: Relić *et al.*, 1994; WO 94/00466; NodRm-Faktoren: WO 91/15496). Secreted Nod factors act in turn as signal molecules that allow rhizobia to enter young root hairs of a host plant, and induce root-cortical cell division that will produce the future nodule. Invaginated rhizobia progress towards the forming nodule within infection threads that are synthesized by the plant cells. Bacteria are then released into the cytoplasm of dividing nodule cells where they differentiate into bacteroids capable of fixing atmospheric nitrogen.

With respect to regulation of the nodulation genes, other regulatory genes with similarities to *nodD1* (genes that belong to the *lysR* family) have been identified in various strains (Davis and Johnston, 1990). The function of those genes, called *nodD2*, *nodD3* or *syrM*, is only partially understood. Some *nodD* genes have been described (WO 94/00466; CA 1314249; WO 87/07910; US 5023180). Also, recombinant DNA molecules including the consensus sequence of the promoters of *nodD1*-regulated genes, called *nod*-boxes (Fisher and Long, 1993), have been disclosed (US 54847186; US 5085588). Finally, recombinant plasmids with the *nodABC* genes or, in one case (*Bradyrhizobium japonicum*), a sequence influencing host specificity have been disclosed (US 5045461; US 4966847).

(B) Symbiotic nitrogen fixation

Inside the nodules, rhizobia differentiate into bacteroids that express the enzymatic complex (nitrogenase) required for the reduction of atmospheric nitrogen into ammonia. The nitrogenase is encoded by three genes *nifH*, *nifD* and *nifK* which are well conserved in nitrogen fixing organisms (Badenoch-Jones *et al.*, 1989). Many additional loci are necessary for functional nitrogenase activity. Those originally identified in *Klebsiella pneumoniae* are known as *nif* genes, whereas those found only in *Rhizobium* strains are described as *fix* genes (Fischer, 1994). Some of these gene products are required for the biosynthesis of cofactors, the assembly of the enzymatic complex or play regulatory and different accessory roles (oxygen-limited respiration, etc.). Many of these genes are less conserved among the various rhizobial strains and in some cases their function is still not fully understood. The high sensitivity of the nitrogenase complex to free oxygen requires a very strict control of most *nif* and *fix* gene expression. In this respect, the FixL, FixJ, FixK, NifA and RpoN proteins have been identified in representative *Rhizobium* species as the major regulatory elements that, in microanaerobic conditions, activate the synthesis of the nitrogenase complex (Fischer, 1994). Recombinant DNA molecules containing *nif* genes/promoters have been disclosed: *nifH* promoters of *B. japonicum* (US 50008194), *nifH* and *nifD* promoter of *R. japonicum* (EP 164245), *nifA* of *B. japonicum* and *R. meliloti* (EP 339830), *nifHDK* and hydrogen-uptake (*hup*) genes of *R. japonicum* (EP 205071).

Many more genetic determinants play a significant role in the *Rhizobium*-legume symbiosis. Genes (*exo*, *lps* and *ndv* genes) involved in the production of extracellular polysaccharides (EPS), lipopolysaccharides (LPS) and cyclic glucanes of rhizobia play an essential role in the symbiotic interaction (Long *et al.*, 1988; Stanfield *et al.*, 1988). Mutation in these genes negatively influences the development of functional nodules. In this respect, some exopolysaccharides of the NGR234 derivative strain ANU280, have been disclosed (WO 87/06796). Although Nod factors seem to play a key role in the nodulation process, experimental data indicate that other signal molecules produced by the bacterial symbionts are required for functional symbiosis and may play a role in coordinating various steps such as the controlled invasion process, the release of rhizobia from the infection thread into the plant cell cytoplasm, the bacteroid differentiation process, etc. Moreover, the need for rhizobia to survive in the rhizosphere and to compete adequately with other microorganisms requires many more unidentified genes that, although they may not be characterised as proper symbiotic loci, do affect the efficiency of the various strains to induce functional nitrogen fixing symbiosis in field conditions. Finally, in our view genetic engineering of improved rhizobial strains cannot be pursued without a more extended knowledge of the structure and complexity of the *Rhizobium* symbiotic genome.

In this respect we decided to determine the complete DNA sequence of a symbiotic plasmid of *Rhizobium* sp. NGR234. In contrast to *Bradyrhizobium* and *Azorhizobium* that carry symbiotic genes on large chromosomes (ca. 8 Mbp) and to *R. meliloti* that harbours two very large symbiotic plasmids of 1.4 and 1.6 Mbp, NGR234 carries a single plasmid of ca. 500 kbp, pNGR234a. Moreover, it has been shown by transfer of pNGR234a into heterologous rhizobia, and even into non-nodulating *Agrobacterium tumefaciens*, that most nodulation functions are encoded by this plasmid (Broughton *et al.*, 1984). The fact that NGR234 is able to interact symbiotically with more plants than any other known strain, and that a complete ordered cosmid library of pNGR234a was available, reinforced NGR234 as the best choice for a large-scale sequencing effort on a symbiotic plasmid (Perret *et al.*, 1991; Freiberg *et al.*, in press).

Automated fluorescent methods have been used to sequence cosmids from eukaryotic organisms, including *Saccharomyces cerevisiae* (Levy, 1994), *Caenorhabditis elegans* (Sulston *et al.*, 1992), *Drosophila melanogaster* (Hartl and Palazzolo, 1993), and *Homo sapiens* (Bodmer, 1994), as well as chromosomes from the prokaryotes *Haemophilus influenzae* (Fleischmann *et al.*, 1995) and *Mycoplasma genitalium* (Fraser *et al.*, 1995). In most large-scale sequencing centres this technology is based mainly on the shotgun approach. After random fragmentation of DNA (e.g. cosmids, bacterial artificial chromosomes (BACs), entire chromosomes) using sonication or mechanical forces, size-selected fragments are subcloned into M13 phages, phagemids or plasmids and sequenced by cycle sequencing using dye primers (Craxton, 1993). A disadvantage of this method is that DNA regions with elevated GC contents produce large numbers of compressions (unresolvable foci in sequence gels) in the dye primer sequences leading to several hundred compressions per assembled cosmid sequence. It is known that the use of dye terminators - fluorescently labelled dideoxynucleoside triphosphates - instead of dye primers reduces the number of compressions (Rosenthal and Charnock-Jones, 1993). Therefore, dye terminators are frequently being used for gap closure and proofreading after assembly of the shotgun data.

To sequence GC-rich cosmids with the highest accuracy, the effectiveness of shotgun sequencing with dye terminators in comparison to dye primer sequencing was investigated. To improve the incorporation of dye terminators into DNA, a modified *Taq* DNA polymerase carrying a single mutation was used (Tabor and Richardson, 1995). This enzyme has properties similar to a thermostable "sequenase" and is commercially available as Thermo Sequenase (Amersham, Buckinghamshire, UK) or AmpliTaq FS (Perkin-Elmer, Foster City, CA, USA). Concentrations of dye terminators needed in the cycle sequencing reactions can be reduced by 20 - 250 times. It was found that dye terminator shotgun sequencing leads to compression-free raw data that can be assembled much faster than shotgun data mainly obtained by dye primer sequencing. This strategy thus allows a several-fold increase in speed to sequence individual

cosmids. This was demonstrated by comparing assembly of the sequence data of two cosmids from pNGR234a generated by different chemistries: Cosmid pXB296 was sequenced with dye terminators, whereas data for pXB110 were obtained using the common dye primer method. Also disclosed is the analysis of the entire pXB296 sequence.

Moreover, the dye terminator shotgun sequencing strategy used to generate the sequence data for pXB296 was also used to sequence all the other remaining overlapping cosmids of the plasmid pNGR234a. In summary, 20 cosmids have been sequenced together with two PCR products and a subcloned DNA fragment derived from a cosmid identified as pXB564 in order to generate the plasmid's complete nucleotide sequence.

After its assembly, the analysis of the entire nucleotide sequence of pNGR234a, especially the determination of putative coding regions and the prediction of their expressible proteins and putative functions, was performed. Initially, analysis of the region covered by cosmid pXB296 was extended to cosmids pXB368 and pXB110. Thus, in approximately 100 kb of the plasmid (position 417,796 - 517,279) most ORFs and their deduced proteins with different putative functions were predicted. Subsequently, the rest of pNGR234a was analyzed.

SUMMARY OF THE INVENTION

The present invention provides the complete nucleotide sequence of symbiotic plasmid pNGR234a or degenerate variants thereof of *Rhizobium* sp. NGR234.

The present invention also contemplates sequence variants of the plasmid pNGR234a altered by mutation, deletion or insertion.

Also encompassed by the present invention are each of the ORFs derivable from the nucleotide sequence of pNGR234a or variants thereof.

In a preferred embodiment, the ORFs derived from the nucleotide sequence of pNGR234a encode the functions of nitrogen fixation, nodulation, transportation, encapsulation, secretion (of proteins), transcriptional regulation, DNA-binding, peptidolysis, proteolysis, transposition, integration, rhizopine biosynthesis, or encode proteins exhibiting similarities to proteins of amino acid metabolism or related ORFs, or proteins putatively involved in the degradation of xenobiotic compounds.

In another preferred embodiment, the ORFs are under the control of their natural regulatory elements or under the control of analogues to such natural regulatory elements.

The present invention also provides the sequences of the intergenic regions of pNGR234a which, in a preferred embodiment, are regulatory DNA sequences or repeated elements.

The present invention also contemplates the use of the disclosed nucleotide sequences or ORFs in the analysis of genome structure, organisation or dynamics.

Also provided by the present invention is the use of the nucleotide sequences or ORFs in the subcloning of new nucleotide sequences. In a preferred embodiment, the new nucleotide sequences are coding sequences or non-coding sequences.

In yet a further preferred embodiment, the nucleotide sequences or ORFs are used in genome analysis and subcloning methods as oligonucleotide primers or hybridization probes.

The present invention further provides proteins expressible from the disclosed nucleotide sequences or ORFs.

Also contemplated by the present invention is the use of the disclosed nucleotide sequences, individual ORFs or groups of ORFs or the proteins expressible therefrom in the identification and classification of organisms and their genetic information, the identification and characterisation of nucleotide sequences, the identification and characterisation of amino acid sequences or proteins, the transportation of compounds to and from an organism which is host to said nucleotide sequences, ORFs or proteins, the degradation and/or metabolism of organic, inorganic, natural or xenobiotic substances in a host organism, or the modification of the host-range, nitrogen fixation abilities, fitness or competitiveness of organisms.

The present invention also provides plasmid pNGR234a of *Rhizobium* sp. NGR234 comprising the disclosed nucleotide sequence or any degenerate variant thereof.

The present invention also provides a plasmid harbouring at least one of the disclosed ORFs or any degenerate variant thereof.

The plasmids of the invention may be produced recombinantly and/or by mutation, deletion, insertion or inactivation of an ORF, ORFs or groups of ORFs.

The present invention also provides the use of the disclosed plasmids or variants thereof in obtaining a synthetic minimal set or ORFs required for functional *Rhizobium*-legume symbiosis, the modification of the host-range of rhizobia, the augmentation of the fitness or competitiveness of *Rhizobium* sp. NGR234 in the soil and its nodulation efficiency on host plants, the introduction of desired phenotypes into host plants using the disclosed plasmids as stable shuttle systems for foreign DNA encoding said desired phenotypes, or the direct transfer of the disclosed plasmids into rhizobia or other microorganisms without using other vectors for mobilization.

The nucleotide sequences of the present invention were advantageously obtained using known cycle sequencing

methods. The preferred dye terminator/thermostable sequenase shotgun sequencing method used to generate the nucleotide sequences of the present invention, when applied to cosmids and when compared to other sequencing methods, was shown to yield sequence reads of the highest fidelity. Consequently, the speed of assembly of particular cosmids was increased, and the resultant high-quality sequences required little editing or proofreading. Thus, the preferred sequencing method described herein was successfully used to generate the complete nucleotide sequence of all the overlapping cosmids of plasmid pNGR234a, thereby resulting in the assembly of the complete sequence of the plasmid.

The complete sequence of pNGR234a is disclosed for the first time in this application, as are the majority of the ORFs predicted within the sequence. Putative functions have been ascribed to the novel and inventive ORFs disclosed herein and the proteins for which they code.

DETAILED DESCRIPTION OF THE INVENTION

Comparison of Different Shotgun Sequencing Strategies

The following is a more detailed description of certain key aspects of the present invention.

GC-rich cosmids were examined to investigate whether they could be sequenced much more efficiently using dye terminators throughout the shotgun phase instead of dye primers. As a test case, cosmid pXB296 with a GC content of 58 mol% from pNGR234a, the symbiotic plasmid of *Rhizobium* sp. NGR234, was exclusively sequenced using dye terminators in combination with a thermostable sequenase [Thermo Sequenase (Amersham)]. Another rhizobial cosmid with identical GC content, pXB110, was sequenced using traditional dye primer chemistry and *Taq* DNA polymerase.

Using the dye terminator/thermostable sequenase shotgun strategy, it was shown that most, if not all, compressions could be resolved and reads were produced with the highest fidelity among all sequencing chemistries tested. As a result, a much faster assembly of cosmid pXB296 in comparison to pXB110 was obtained. The shotgun data could be assembled into a high-quality sequence without extensive editing and proofreading. By measuring the error rate in overlapping regions between individual cosmids from pNGR234a, as well as the cosmid vector sequence itself (data not shown), it was estimated that the accuracy of the pXB296 sequence is higher than 99.98%. Using other thermostable sequenases such as AmpliTaq FS (Perkin-Elmer), similar results were expected because thermostable sequenases have similar properties.

Dye primer chemistry in combination with Thermo Sequenase was also examined. Although the peak uniformity of signals was much improved over dye primer/*Taq* DNA polymerase data, the number of compressions in GC-rich shotgun reads was not reduced significantly. Compressions in shotgun raw data enormously increase the overall effort of editing, proofreading, and finishing a cosmid as shown for pXB110 (Table 1).

Because of their longer reading potential, dye primer reads are helpful for gap closure. However, using ABI 373A sequencers (Applied Biosystems, Inc. (ABI), Perkin-Elmer, Foster City, CA, USA), dye primer reads are, on average, only ~50 bases longer than dye terminator reads.

Using the experimental conditions of the present invention, shotgun sequencing with dye terminators and a thermostable sequenase is superior because for GC-rich cosmid templates it removes most of the compressions and this leads to a several-fold improvement in assembling and finishing of cosmid-sized projects. Although dye terminators are slightly more expensive than dye primers, the overall saving in time for finishing projects has, in our experience, a much greater effect on general costs.

It has been shown that the strategy of the present invention is effective for high-throughput shotgun sequencing of GC-rich templates. This strategy was therefore used to sequence the remaining 19 overlapping cosmids of the symbiotic plasmid pNGR234a of *Rhizobium* sp. NGR234. In total, 20 cosmids, two PCR products (1.5 and 2.0 kb in length) and a 1.5 kb restriction fragment were sequenced in order to generate the complete pNGR234a sequence (Figure 4).

Genetic Organization of pXB296

All 28 predicted open reading frames (ORFs) in pXB296 (Figure 1) show significant homologies to database entries. The first putative gene cluster (cluster I) containing ORF1 to ORF5 corresponds to various oligopeptide permease operons (Hiles *et al.*, 1987; Perego *et al.*, 1990). Only ORF5 shows

Table 1

Comparison of the assembly of the sequence data from cosmids pXB296 (dye terminator shotgun reads) and pXB110 (dye primer shotgun reads)		
Data assembly	pXB296	pXB110
Average length of the shotgun reads (bases)	332	378
No. of shotgun reads used for assembly	786	899
No. of shotgun reads assembled with 4% mismatch ^a	736	308
No. of shotgun reads assembled with 25% mismatch ^a	775	879
No. of contigs ^b longer than 1 kbp	3	25
No. of contigs left after editing ^c	2	4
No. of additional reads (gap closure and proofreading) ^d	32	191
Total length of cosmid insert (bp)	34,010	34,573
Sequencing redundancy (per bp)	8.0	10.5

^aAssembling program: XGAP; principal autoassembling conditions: normal shotgun assembly, joins permitted, minimum initial match = 15, maximum no. of pads per reading during the alignment procedure = 8, maximum no. of pads per reading in contig to align any new reading = 8, alignment mismatches 4% and 25%, respectively.

^bContiguous parts of sequence created by overlapping reads.

^cLengths of contigs: 6-10 kbp (pXB296); 2-12 kbp (pXB110).

^dReads necessary for closing gaps and making single-stranded regions double-stranded by primer walking on selected templates and, in case of pXB110, for solving ambiguities (compressions) by the resequencing of clones with universal primer and dye terminators.

homology to a gene from a different bacterium, *Bacillus anthracis* (Makino *et al.*, 1989). Each homologue encodes membrane-bound or membrane-associated proteins suggesting that all five ORFs are involved in oligopeptide permeation.

Organization of the predicted gene cluster IV, including the *nifA* homologue ORF16 (*fixABCX*, *nifA*, *nifB*, *fdxN*, ORF, *fixU* homologues, position 16,746 - 24,731), the predicted locations of the σ^{54} -dependent promoters and the *nifA* upstream activator sequences (Figure 1), correspond to the organization found in *Rhizobium meliloti* and *Rhizobium leguminosarum* bv. *trifolii*. (Iismaa *et al.*, 1989; Fischer, 1994). *NifA* is a positive transcriptional activator (Buikema *et al.*, 1985), whereas *nif* and *fix* genes are essential for symbiotic nitrogen fixation. Identification of σ^{54} -dependent promoter sequences, together with the upstream activator motifs upstream of ORF21, ORF22, and ORF23, suggests that these ORFs may play an important, but still undefined, role in symbiosis.

Inevitably, large-scale sequencing uncovers differences with already published sequences. van Slooten *et al.* (1992) cloned a 5.8 kb *EcoRI* fragment from *Rhizobium* sp. NGR234 and sequenced 2067 bp by manual radioactive methods (EMBL accession no. S38912). This sequence exhibits 2.4% mismatches with the corresponding sequence in pXB296. It contains the gene *dctA* (encoding a C₄-dicarboxylate permease), which is 144 bases shorter than in pXB296. In this respect, a single nucleotide deletion in position 29,248 of the cosmid sequence close to the 3' end of the gene causes a frameshift leading to a DctA product extended by 48 residues. van Slooten *et al.* (1992) also failed to identify the *nifQ* homologue, ORF23 (position 27,169 - 27,861), presumably because they overlooked a small *XhoI* fragment located between positions 27,349 and 27,536 on pXB296. Expression studies allowed these investigators to define a putative σ^{54} -dependent promoter in a 1.7 kb *SmaI* fragment (position 27,094 - 28,818 in pXB296). This fragment stretches from the upstream region of ORF23 to the 5' part of *dctA*. The 58 bp intergenic region between ORF23 and *dctA* contains a stem-loop structure but no obvious promoter sequence. Possibly the promoter that controls *dctA* is located upstream of ORF23 (e.g. the minimal consensus sequence included in GGGGGCACAATTGC at position 27,098 - 27,111). Although clones containing *dctA* complemented mutants of *R. meliloti* and *R. leguminosarum* for growth on dicarboxylates, the growth of the NGR234 *dctA* deletion mutant was not affected (van Slooten *et al.*, 1992). Nevertheless, this mutant was unable to fix nitrogen in nodules. Because *dctA* is now possibly part of a larger transcription unit, the symbiotic phenotype may also result from the inactivation or downstream genes.

Interestingly, the GC content of the predicted pXB296 ORFs ranges from 53.3 mol% to 64.6 mol%, with an overall cosmid GC content of 58.5 mol%. Genomes of *Azorhizobium*, *Bradyrhizobium*, and *Rhizobium* species have GC con-

tents of 59 mol% to 65 mol% (Madmanabhan *et al.*, 1990), with 62 mol% reported for *Rhizobium* sp. NGR234 (Broughton *et al.*, 1972). Although pXB296 covers <7% of the complete symbiotic plasmid sequence, its lower overall GC value suggests that symbiotic genes might have evolved by lateral transfer from other organisms. In this case, methods of the type applied in the present invention will become even more relevant in sequencing the whole genome.

Genetic Organization of the 100 kb region covered by cosmids pXB296, pXB368 and pXB110

Extending the analysis of pXB296 to a 100 kb region stretching from position 417,796 to 517,279 on the symbiotic plasmid pNGR234a has led to the assignment of the 76 ORFs listed in Table 4 (excluding the first incomplete ORF noted in the analysis of pXB296 ("ORF1" of Table 3)). The ORFs K1 to L4 are identical to the ORFs 2 to 28 of the analysis of pXB296 (Table 3). The cosmid pXB110, which was sequenced with the dye primer shotgun sequencing strategy in order to compare it with the dye terminator shotgun sequencing strategy used to sequence cosmids pXB296 and pXB368, covers nearly this entire region. A PCR product and a restriction fragment of cosmid pXB564 also had to be sequenced in order to fill in the gap from position 480,607 to 483,991 between cosmids pXB368 and pXB110 (Figure 4). Among the predicted ORFs, 7 ORFs and their deduced proteins show no homologies to database entries. The other predicted ORFs and their deduced proteins do exhibit such homologies and therefore play putative roles in nitrogen fixation (ORFs K11 to K19, K22, L8 to L12, L23 and L24), nodulation (ORFs M15 and M20), transportation (ORFs K1 to K4, K23 and L25), secretion of proteins or other biomolecules (ORFs M21 to M27), transcriptional regulation/DNA binding (ORFs L16 and M6), in amino acid metabolism or metabolism of amino acid derivatives (ORFs K5, K6, K8, L17, L18 and M11 to M14), degradation of xenobiotic compounds (ORFs L1 to L3), in peptidolysis/proteolysis (ORFs L14 and L15) or transposition (ORFs K7, K9 and K10). The role of some ORFs like the luciferase-like ORFs (L4 and L19) in rhizobia is still not clear. In the 100 kb region, the duplication of a 5 kb sequence (position 451,886 to 456,157 and 483,764 to 488,035) including the genes *nifHDK* is remarkable. These genes encode the basic subunits of the nitrogenase. Furthermore, the transcriptional regulator *nodD2* is very interesting because its role seems not to be identical to a previously identified *nodD2* in a closely related strain (Appelbaum *et al.*, 1988; data not shown). Also the *pimA*-homologous ORF M6 putatively plays an important role in regulating symbiotic processes because a *nod* box (binding region for the basic regulator *nodD1*; Fisher and Long, 1993) is located upstream of this ORF (position 493,962 to 494,000). Finally, the presence of ORFs (M21 and M23 to M26) homologous to type III secretion proteins, which have only been known previously in plant or animal/human pathogenic bacteria, shows that there only seems to be a subtle difference between symbiotic and pathogenic abilities of microorganisms.

In a second stage, the remaining 436 kb of pNGR234a were analyzed. Several ORFs and their deduced proteins were identified that belong to functional groups not previously identified in the analysis of cosmids pXB296, pXB368 and pXB110 (replication of the plasmid, conjugal transfer of the plasmid, functions in oligosaccharide biosynthesis and cleavage, functions in sugar or sugar-derivative metabolism, functions in lipid or lipid-derivative metabolism, functions in chemoperception/chemotaxis, functions in biosynthesis of cofactors, prosthetic groups and carriers, etc.).

Although functional analyses of selected ORFs in pNGR234a still have to be performed, large-scale sequencing gives a global picture of their genomic organization and possible roles. Determination of putative functions of predicted genes by homology searches and identification of sequence motifs (promoters, *nod* boxes, *nifA* activator sequences, and other regulatory elements) will aid in finding new symbiotic genes. High-fidelity sequence data covering long stretches of the genome are a prerequisite for these studies. The use of the dye terminator/thermostable sequenase shotgun approach has allowed the completion of the entire ~500 kb sequence of pNGR234a and has opened up new avenues for the genetic analysis of symbiotic function.

Example 1

GENERAL METHODS

Bacteria and Plasmids

Escherichia coli was grown on SOC, in TB or in twofold YT medium (Sambrook *et al.*, 1989). The cosmid clones pXB296 and pXB110 (Perret *et al.*, 1991) were raised in *E. coli* strain 1046 (Cami and Kourilsky, 1978). Subclones in M13mp18 vectors (Yanisch-Perron *et al.*, 1985) were grown in *E. coli* strain DH5 α F'IQ (Hanahan, 1983).

Construction of Cosmid Libraries

Cosmid DNA was prepared by standard alkaline lysis procedures followed by purification in CsCl gradients (Radloff *et al.*, 1967). DNA fragments sheared by sonication of 10 μ g of cosmid DNA were treated for 10 min at 30°C with 30 units of mung bean nuclease (New England Biolabs, Beverly, MA, USA), extracted with phenol/chloroform (1:1), and

precipitated with ethanol. DNA fragments, ranging in size from 1 to 1.4 kbp, were purified from agarose gels using GeneClean II (Bio101, Vista, CA, USA) and ligated into *Sma*I-digested M13pm18. Electroporation of aliquots of the ligation reaction into competent *E. coli* DH5 α F'IQ was performed according to standard protocols (Dower *et al.*, 1988; Sambrook *et al.*, 1989).

M13 Template Preparation

Fresh 1 ml *E. coli* cultures in twofold YT held in 96-deep-well microtiter plates (Beckman Instruments, Fullerton, CA, USA) were infected with recombinant phages from white plaques grown on plates containing X-gal (5-bromo-4-chloroindolyl- β -D-galactoside) and IPTG (isopropyl- β -thiogalactopyranoside). Rapid preparation of ~0.5 μ g of single-stranded M13 template DNA was carried out as follows: 190 μ l portions of the phage cultures grown for 6 hr at 37°C were transferred into 96-well microtiter plates. Lysis of the phages was obtained by adding 10 μ l of 15% (w/v) SDS followed by 5 min incubation at 80°C. Template DNA was trapped using 10 μ l (1 mg) of paramagnetic beads (Streptavidin MagneSphere Paramagnetic Particles Plus M13 Oligo, Promega, Madison, WI, USA) and 50 μ l of hybridization solution [2.5 M NaCl, 20% (w/v) polyethylene glycol (PEG-8000)] during an annealing step of 20 min at 45°C. Beads were pelleted by placing microtiter plates on appropriate magnets and washing three times with 100 μ l of 0.1-fold SSC. The DNA was recovered in 20 μ l of water by a denaturation step of 3 min at 80°C. When required, larger amounts of single-stranded recombinant DNA (>10 μ g) were purified using QIAprep 8 M13 Purification Kits (Qiagen, Hilden, Germany) from 3 ml of supernatant of phage cultures grown for 6 hr at 37°C.

Sequencing

Two sequencing methods were used: dye terminator and dye primer cycle sequencing, each in combination with AmpliTaq DNA polymerase (Perkin-Elmer) and Thermo Sequenase (Amersham). All reactions, including ethanol precipitation, were performed in microtiter plates. Reagents were pipetted using 12-channel pipettes. Where necessary, sequencing reaction mixtures, including enzymes, were pipetted into the plates in advance and held at -20°C until needed.

Dye Terminator Cycle Sequencing

For dye terminator/AmpliTaq DNA polymerase sequencing, 0.5 μ g of template DNA, and the PRISM Ready Reaction DyeDeoxy Terminator Cycle Sequencing Kit (Perkin-Elmer) were used. Cycle sequencing was performed in microtiter plates using 25 PCR cycles (30 sec at 95°C, 30 sec at 50°C, and 4 min at 60°C). Prior to loading the amplified products on electrophoresis gels, unreacted dye terminators were removed using Sephadex columns scaled down to microtiter plates (Rosenthal and Charnock-Jones, 1993).

Dye terminator/Thermo Sequenase sequencing was performed using the same experimental conditions except that the reaction mix contained 16.25 mM Tris-HCl (pH 9.5), 4.0 mM MgCl₂, 0.02% (v/v) NP-40, 0.02% (v/v) Tween 20, 42 μ M 2-mercaptoethanol, 100 μ M dATP/dCTP/dTTP, 300 μ M dITP, 0.017 μ M A/0.137 μ M C/0.009 μ M G/0.183 μ M T from Taq Dye Terminators (Perkin-Elmer; no. A5F034), 0.67 μ M primer, 0.2-0.5 μ g of template DNA, and 10 units of Thermo Sequenase (Amersham) in a 30 μ l reaction volume. Unincorporated dye terminators were removed from reaction mixtures by precipitation with ethanol.

Dye Primer Cycle Sequencing

Dye primer/AmpliTaq DNA polymerase sequencing reactions were performed according to the instructions accompanying the Taq Dye Primer, 21M13 Kit (Perkin-Elmer). Cycle sequencing was carried out on 0.5 μ g of template DNA with 19 PCR cycles (30 sec at 95°C, 30 sec at 50°C, and 90 sec at 72°C) followed by six cycles, each consisting of 95°C for 30 sec and 72°C for 2.5 min. Prior to electrophoresis, the four base-specific reactions were pooled and precipitated with ethanol.

Identical PCR conditions and the Thermo Sequenase Fluorescent Labelled Primer Cycle Sequencing Kit (Amersham) were used for dye primer/Thermo Sequenase sequencing reactions.

Sequence Acquisition and Analysis

Gel electrophoresis and automatic data collection were performed with ABI 373A DNA sequencers (Perkin-Elmer). After removing cosmid vector and M13mp18 sequences from the shotgun sequence data, the data were assembled using the program XGAP (Dear and Staden, 1991) and edited against the fluorescent traces. To close remaining gaps, to make single-stranded regions double-stranded, and to clarify ambiguities, additional cycle sequencing reactions with

selected shotgun templates were carried out using either custom-made primers (primer-walks) or universal primer.

The complete double-stranded DNA sequence of cosmid pXB296 was analyzed using programs from the Wisconsin Sequence Analysis Package (v. 8, Genetics Computer Group, Madison, WI, USA). Homology searches were performed with BLAST (v. 1.4; Altschul *et al.*, 1990) and FASTA (v. 2.0; Pearson and Lipman, 1988). Several nucleotide and protein databases were screened (GenBank/Genpept, SwissProt, EMBL, and PIR). Identities and similarities between homologous amino acid sequences were calculated with the alignment program BESTFIT (Smith and Waterman, 1981).

Example 2

Comparison of Fluorescent Traces Created by Different Cycle Sequencing Methods

When using a thermostable sequenase [Thermo Sequenase (Amersham)], the concentrations of dye terminators (Perkin-Elmer) can be reduced by 20- to 250-fold in comparison to the concentrations needed for *Taq* DNA polymerase without compromising the quality of the sequencing results (Table 2).

To compare the dye terminator and dye primer cycle sequencing procedures, representative templates derived from the pXB296 library were sequenced by both methods, each performed with Thermo Sequenase and *Taq* DNA polymerase (Figure 2). In general, dye terminator traces do not contain the many compressions (on average, one compression every 50 bases in single reads) that are common with dye

Table 2

Concentrations (in μM) of dye terminators in each cycle sequencing reaction with two different thermostable DNA polymerases			
Dye terminator	AmpliTaq DNA polymerase	Thermo Sequenase DNA polymerase	Dilution factor for dye terminators ^a
A <i>Taq</i>	0.751	0.017	40
C <i>Taq</i>	22.500	0.137	160
G <i>Taq</i>	0.200	0.009	20
T <i>Taq</i>	45.000	0.183	250

^aThermo Sequenase vs. AmpliTaq.

primers if mixes do not contain nucleotide analogues like deoxyinosine or 7-deaza-deoxyguanosine triphosphates or if sequencers are used without active heating systems. In addition, dye terminator traces obtained with Thermo Sequenase show more uniform signal intensities over those obtained with *Taq* DNA polymerase, thus resulting in a reduced number of weak and missing peaks (e.g. a weak G-signal following an A-signal in Thermo Sequenase traces or a weak C-signal following a G-signal in *Taq* DNA polymerase traces). Using ABI 373A sequencers, errors in automatic base-calling of Thermo Sequenase/dye terminator scans only arise after 300-350 bases. The average number of resolved bases in dye primer gels (378 bases) is 46 bases longer than in those produced with dye terminators (332 bases). Furthermore, in Thermo Sequenase/dye primer sequences the peaks are very regular and the number of stops and missing bases decreases in comparison to *Taq* DNA polymerase/dye primer electropherograms. The number of compressions, however, is not significantly reduced.

Example 3

Shotgun Sequencing of Entire Cosmids Using Dye Terminators or Dye Primers

To compare the efficiency of both methods, cosmid pXB296 of pNGR234a was shotgun sequenced using a combination of dye terminators and thermostable sequenase (Thermo Sequenase), whereas another cosmid, pXB110, was sequenced using a combination of dye primers and *Taq* DNA polymerase (Table 1). Over 93% (736 clones) of 786 dye terminator reads of pXB296 were accepted by XGAP with a maximal alignment mismatch of 4%. By increasing this level to 25%, so that most of the remaining data could be included in the assembly, 775 reads led to three 6 to 10 kbp stretches of contiguous sequence (contigs), two of which were joined after editing. To close the last gap and to complete single-stranded regions with data derived from the opposite strand, only 32 additional dye terminator reads using cus-

tom-made primers were required. It took <1 week to assemble and finalize the 34,010 bp DNA sequence of pXB296 (EMBL accession no. Z68203; eightfold redundancy; GC content, 58.5 mol%).

In contrast, only 308 (34%) of 899 shotgun reads obtained by *Taq* DNA polymerase/dye primer cycle sequencing of pXB110 were included in the first assembly (4% alignment mismatch). At the 25% alignment mismatch level, 879 reads were assembled, leading to 25 short contigs (1-2 kbp). These contigs had to be edited extensively in order to join most of them. "Primer walks", covering gaps and complementing single-stranded regions, were not sufficient to clarify all the remaining ambiguities in the assembled sequence. Every 100-150 bp, a compression in one strand could not be resolved by sequence data from the complementary strand. Therefore, it was necessary to resequence clones using dye terminators and universal primer. In total, 191 additional dye terminator reads had to be created. As a result, assembling and finalizing the 34,573 bp sequence of pXB110 (10.5-fold redundancy; GC content, 58.3 mol%) took much more time than pXB296 did.

Example 4

Analysis of Cosmid pXB296

Putative ORFs were located on the 34,010 bp sequence of pXB296 using the programs TESTCODE (Fickett, 1982) and CODONPREFERENCE (Gribkov *et al.*, 1984), the latter in combination with a codon frequency table based on previously sequenced genes of *Rhizobium* sp. NGR234 (as well as the closely related *R. fredii*). All 28 ORFs and their deduced amino acid sequences exhibited significant homologies to known genes and/or proteins. The positions of the ORFs along pXB296, as well as the best homologues, are displayed in Table 3 and Figure 1. Ribosomal binding site-like sequences (Shine and Dalgarno, 1974) precede each putative ORF except for ORF9 (position 11,214-12,455). If one disregards the homology to known glutamate dehydrogenases in the first 32 amino acids deduced from this ORF, a downstream alternative start codon (position 11,220) preceded by a Shine-Dalgarno sequence can be identified. Most of the ORFs are organised in five clusters (ORFs with only short intergenic spaces or overlaps between them). Cluster I, containing ORF1 to ORF5, encodes proteins homologous to *trans*-membrane and membrane-associated oligopeptide permease proteins and to a *Bacillus anthracis* encapsulation protein. Cluster II, includes ORF6 and ORF7, which are homologous to aminotransferase and (semi)aldehyde dehydrogenase genes. Homologies to transposase genes [ORF8; cluster III (ORF10 and ORF11)] and to various *nif* and *fix* genes [cluster IV (ORF12 to ORF20); ORF23, part of cluster V] are also reported.

Presumed promoter and stem-loop sequences that might represent ρ -independent terminator-like structures (Platt, 1986) are shown in Figure 2. Significant σ^{54} -dependent promoter consensus sequences (5'-TGGCACG-N₄-TTGC-3'; Morett and Buck, 1989), as well as *nifA* upstream activator sequences (5'-TGT-N₁₀-ACA-3'; Morett and Buck, 1988), are found upstream of the *nifB* homologue ORF15, the *fixA* homologue ORF20, ORF21, ORF22, and ORF23. ORF23 is part of cluster V in pXB296, which includes the *dctA* gene of *Rhizobium* sp. NGR234 (van Slooten *et al.*, 1992). Surprisingly, the published *dctA* sequence shows important discrepancies. Therefore, a fragment encompassing this locus was amplified by PCR using NGR234 genomic DNA as template. By sequencing this fragment, the cosmid sequence of the present invention was confirmed.

Table 3. Putative ORFs of pXB296 and homologues of the deduced amino acid sequences to known proteins

ORF ^a	st. ^b	position on cosmid (base no.) ^c	ribosomal binding site: SD-sequence - distance from start codon (bases) - start codon ^d	no. of deduced amino acids	homologous amino acids (position)	homologous protein	length (aa) ^e	function ^f	accession no.	identity (%) ^g	similarity (%) ^g
			SD-sequence: 5' - TAAGGAGGTGA - 3'			name					
ORF1 ^b	+	00001-00625		>207	1-207	OppB	306	oligopeptide	X05491	43	68
ORF2	+	00628-01503	GTATCCGGT-7-ATG	291	2-289	OppC	305	permease	X56347	37	63
ORF3	+	01505-02512	AGCGGAGG-7-ATG	335	8-327	OppD	336	proteinase	X56347	49	69
ORF4	+	02509-03570	TGAAGTGGT-6-ATG	353	2-323	OppF	334		X05491	51	69
ORF5	+	03606-04991	CAAGGA-6-ATG	461	1-458	CapA	411	encapsulation protein	M24150	25	48
ORF6	+	05460-06863	CCGAGAGG-8-ATG	467	1-464	BioA	455	aminotransferase	M29292	29	55
ORF7	+	06888-08426	GCCTTCGG-5-GTG	512	97-509 34-510	ORF ^g GapD	417 482	unknown succinic semialdehyde dehydrogenase	D37877 M38417	36 33	58 57
ORF8	-	09781-10860	GAACTGG-8-ATG	359	72-299	ORF ^g	414	transposase homologue minicircle DNA	X15942	30	48
ORF9	+	11124-12455	?-7-ATG	443	2-443	GLUD1	558	glutamate dehydrogenase	M37154	41	60
ORF10	-	13370-14116	AAAGGA-6-ATG	248	1-245	ORF2 ¹	231	transposase	X79443	45	64
ORF11	-	14128-15672	CATGGAG-7-TTG	514	1-513	ORF1 ¹	558	homologues, IS1162	X79443	41	62
ORF12	-	16712-16942	GAAGGA-8-ATG	76	1-70	FixU	70	unknown	P42710	63	80
ORF13	-	16939-17265	ACAAGAGG-7-ATG	109	1-79 15-107	ORF2 ¹ NifZ	>78 159	unknown involved in FeMo-cofactor synthesis	X07567 M20568	53 39	81 56
ORF14	-	17349-17543	CCAGGAG-9-ATG	64	1-64	FdxN	64	ferredoxin-like	M21841	80	87
ORF15	-	17585-19066	AGTGGAG-7-ATG	493	1-493	NifB	490	involved in FeMo-cofactor synthesis	M15544	73	84
ORF16	-	19292-20962	ATTGG-12-ATG	556	9-556	NifA	541	transcriptional regulator	X02615	59	72
ORF17	-	21129-21422	AGGGGAG-7-ATG	97	1-97	FixX	98	required for	M15546	84	87
ORF18	-	21437-22744	AACTGAGGT-7-ATG	435	1-435	FixC	435	nitrogen	M15546	83	90
ORF19	-	22755-23864	ATAGGAG-6-ATG	369	18-369	FixB	353	fixation	M15546	79	89
ORF20	-	23874-24731	TAAAGAG-5-ATG	285	1-285	FixA	292		M15546	74	85
ORF21	-	25148-25468	CCAGGAG-10-ATG	106	1-106	ORF118 ¹	108	unknown	X13691	55	71
ORF22	-	26145-26711	GAAGGAG-9-ATG	188	9-199 1-173	- -	241 166	hypothetical protein peroxisomal protein	U32739 U11244	47 32	64 57

Table 4. List of the 76 predicted ORFs in pNGR234a between position 41796 - 517279

ORF ^a	func- tional name	st. ^b	position on pNGR234a (base no.) ^c	no. of deduced amino acids	homo- logous amino acids (position)	homologous protein			U %	S/ %	protein type
						name	length (aa) ^e	accession no.			
K1		+	41796-418671	291	1-289	OppC	303	U02099	37	63	oligopeptide permease protein
K2		+	418673-419680	335	8-327	OppL	336	X56347	49	69	oligopeptide permease protein
K3		+	419677-420738	353	2-323	OppF	334	X05491	51	69	oligopeptide permease protein
K4		+	420774-422159	461	1-458	CapA	411	M24150	25	48	encapsulation protein-like
K5		+	422628-424031	467	1-464	BioA	455	M29292	29	55	aminotransferase-like
K6		+	424056-425594	512	97-509	ORF	417	D37877	36	58	(semi)aldehyde dehydrogenase-like
K7		-	426949-428028	359	72-299	Tnp	414	X15942	30	48	transposase homologue
K8		+	428792-429623	443	2-443	GLUD1	558	M37154	41	60	glutamate dehydrogenase-like
K9		-	430538-431284	248	1-245	ORF2	231	X79443	45	64	transposase homologue
K10		-	431296-432840	514	1-514	Tnp	518	L09108	44	66	transposase homologue
K11		-	433880-434110	76	1-70	FixU	70	P42710	63	80	unknown function
K12		-	434107-434433	109	1-79	ORF2	>78	X07567	53	81	unknown function
K13		-	434517-434711	64	1-64	FdxN	64	M21841	80	87	ferredoxin/ferredoxin-like
K14	nifB	-	434753-436234	493	1-493	NifB	490	M15544	73	84	involved in FeMo cofactor biosynthesis
K15	nifA	-	436460-438130	556	9-556	NifA	541	X02615	59	72	positive regulator of nif/fix and additional genes
K16	nifX	-	438297-438590	97	1-97	FixX	98	M15546	84	87	required for nitrogenase activity
K17	nifC	-	438605-439912	435	1-435	FixC	435	M15546	83	90	required for nitrogenase activity
K18	nifB	-	439923-441032	369	18-369	FixB	353	M15546	79	89	required for nitrogenase activity
K19	nifA	-	441042-441899	285	1-278	FixA	279	L11081	79	87	required for nitrogenase activity
K20		-	442316-442636	106	1-106	ORF118	108	X13691	55	71	unknown function
K21		-	443313-443879	188	33-187	ORF7	>159	X72888	66	79	unknown function
K22		+	444337-445029	230	1-167	NitQ	167	X13303	37	57	ferredoxin-like
K23	dicA	+	445088-446602	504	1-454	DctA1	456	S38912	97	98	C ₄ -dicarboxylate transport protein
L1		+	446599-447843	414	2-414	CamC	415	M12546	34	53	cytochromeP450-like
L2		+	447844-448500	218	30-190	LinA	155	D90355	27	51	γ-hexachlorocyclohexane-dechlorinase-like
L3		+	448497-450203	568	29-270	ORF4	250	X79863	38	62	pulvate protein with degradative function
L4		+	450341-451396	351	297-535	LuxA	355	M10961	21	47	luciferase or subunit-like

L5	nifH	+	451593-452883	296	1-296	NifH	296	M26961	>99	>99	Fe protein of nitrogenase
L6	nifD	+	452880-454494	504	199-393	NifD	>195	M26962	99	>99	α subunit of MoFe protein of nitrogenase
L7	nifK	+	454590-456131	513	132-195	NifK	>64	M26963	100	>99	β subunit of MoFe protein of nitrogenase
L8		+	456187-457677	496	1-493	NifE	547	X56894	60	77	involved in FeMo cofactor biosynthesis
L9		+	457687-459496	469	1-441	FixF	441	M18272	73	84	involved in FeMo cofactor biosynthesis
L10		+	459093-459573	160	3-158	NifX	159	X17433	48	65	unknown function
L11		+	459579-460657	162	2-156	ORF4	156	X17433	49	70	unknown function
L12		+	460501-460920	139	1-139	NifH	296	M26961	31	58	similar to a part of Fe protein of nitrogenase
L13		+	461228-461545	105	2-102	ORF5	102	M26323	50	68	unknown function
L14		+	463201-464739	512	1-515	bl-MPP	534	X80237	23	47	peptidase-like
L15		+	464736-465079	347	63-446	PP	380	L108471	21	47	processing peptidase-like
L16		+	466590-467021	143	8-132	ORF3	98	L13845	49	69	DNA binding protein-like
L17		+	467758-468891	377	2-371	MonC	407	L17071	27	52	membrane protein from the rhizopane biosynthesis (<i>nif</i> ABH) gene cluster
L18		+	469311-470417	368	10-365	NifJ	356	D14440	32	58	histidyl phosphatase aminotransferase-like
L19		+	470804-471852	341	9-341	LuxA	335	M10961	22	48	luciferase alpha subunit-like
L20		+	473343-473780	145							putative protein
L21		+	473928-475427	499							putative protein
L22		+	475503-475880	125							putative protein
L23		+	476519-476971	150	0-121	NifW	108	M86823	55	65	required for full activity of nitrogenase
L24		+	477135-478298	387	1-387	NifS	387	M86823	59	77	Cysteine desulfurase
L25		+	479145-481136	663	215-623	YnfA	>409	U00008	38	55	alkanoate transporter-like
L26	nifH	+	483871-484761	296	2-296	NifH	296	M26961	>99	>99	Fe protein of nitrogenase
M1	nifD	+	484858-486372	504	199-393	NifD	>195	M26962	99	100	α subunit of MoFe protein of nitrogenase
M2	nifK	+	486568-488009	513	132-195	NifK	>64	M26963	100	>99	β subunit of MoFe protein of nitrogenase
M3		+	488262-488750	162	2-162	ORF4	156	X17433	46	69	putative protein
M4		+	488773-488976	67	1-66	ORF1	69	X55450	39	56	putative protein
M5	nodW2	+	491635-492593	312	1-312	NodD2	312	M18972	99	99	transcriptional regulator of nodulation genes
M6		+	494297-494977	226	1-224	FixA	222	L13395	39	61	response regulator protein
M7		+	495157-496428	423	1-379	GltV	426	V00604	25	49	protein of the general secretion pathway (GSP)
M8		+	496438-497004	188							putative protein
M9		+	497444-498460	338							putative protein
M10		+	498719-499933	404	2-403	ORF1	408	X59939	22	49	putative protein
M11		+	499930-501816	628	20-628	luxC	580	X76100	23	50	aerobactin synthetase subunit-like
M12		+	501816-502955	380							putative protein
M13		+	502952-503962	336	1-308	CysK	308	D26185	37	60	cysteine synthetase-like

M14			503963-505336	457	14-456	TabA	420	M88485	24	48	diaminopimelate decarboxylase-like
M15	noIX		505950-507740	596	1-461	NoIX	471	L12251	99	100	nodulation protein as in <i>R. fredii</i> USDA257, but significantly longer
M16	noIW		508021-508725	234	1-234	NoIW	234	L12251	100		nodulation protein as in <i>R. fredii</i> USDA257
M17	noIB	+	508881-509375	164	1-164	NoIB	164	L12251	99	99	nodulation protein as in <i>R. fredii</i> USDA257
M18	noIT	+	509385-510254	289	1-289	NoIT	289	L12251	97	100	nodulation protein as in <i>R. fredii</i> USDA257
M19	noIU	+	510251-510889	212	1-212	NoIU	212	L12251	99	99	nodulation protein as in <i>R. fredii</i> USDA257
M20	noIV	+	510891-511517	208	1-60	ORF4	65	L12251	100		comprising two nodulation proteins homologous to nodulation proteins of <i>R. fredii</i> USDA257
M21		+	511514-512869	451	73-208	NoIV	135		96	98	putative ATPase involved in typeIII secretion
M22		+	512845-513361	178	10-450	YscN	439	U00998	54	73	putative protein
M23		+	513406-514482	358	21-355	YscQ	307	L25667	24	57	involved in typeIII secretion pathways
M24		+	514475-515143	222	6-217	YscR	217	L25667	46	62	involved in typeIII secretion pathways
M25		+	515143-515418	91	1-87	YscS	88	L25667	28	59	involved in typeIII secretion pathways
M26		+	515427-516245	272	3-272	YscT	261	L25667	29	57	involved in typeIII secretion pathways
M27		+	516242-517279	345	5-339	YscU	345	L25667	30	57	involved in typeIII secretion pathways

a ORF: open reading frame; names K1 to M28 are preliminary; genes written in bold letters are not claimed in the patent application: 1.5, L26, M16, M17, M19.

b SL: (+)/(-)-strand

c no.: number

d first no. represents the most probable start point of a gene (ATG, GTG, TTG are considered start codons)

e aa: amino acids

f Identity (I) and similarity (S) in % have been calculated by the program 'bestfit' (local homology algorithm, Smith and Waterman, 1981) of the Wisconsin Sequence Analysis Package (version 8.0, 'Genetics Computer Group', Madison, USA)

Table 5. ORFs that show 98-100% identity in the nucleotide sequence to ORFs located in pNGR234a and that have already been published in databases:

ORF	organism	EMBL/GenBank accession no.	+	claimed in the patent application/ not claimed in the patent application
<i>dcfA</i>	<i>Rhizobium</i> sp. NGR234	S38912	+	sequencing mistakes in the database entry: the real <i>dcfA</i> in pNGR234a is 144 bases longer (see table 2)
host inducible <i>gcaA</i>	<i>Rhizobium fredii</i> USDA 201#	M19019 RFINP	+	significant difference in pNGR234a (frameshift; see table 2)
<i>nifH</i>	<i>Rhizobium</i> sp. ANU 240*	M26961 RHMNIFKD13	-	
<i>nifD</i> (partially)	<i>Rhizobium</i> sp. ANU 240*	M26961 RHMNIFKD12	+	only part of <i>nifD</i> is in the public database
<i>nifK</i> (partially)	<i>Rhizobium</i> sp. ANU 240*	M26951 RHMNIFKD11	+	only part of <i>nifK</i> is in the public database
<i>nodABC</i>	<i>Rhizobium fredii</i> USDA 257#	M73362 RSNOD2	-	
<i>nodD1</i>	<i>Rhizobium</i> sp. mpik 3030*	Y00059 RSNODD1	-	
<i>nodD2</i>	<i>Rhizobium japonicum</i> USDA 191#	M18972 RHMNODD2M	+	significantly different function of <i>NodD2</i> in NGR234 than in USDA 191 (despite of 98% identity?)
<i>nodS</i>	<i>Rhizobium</i> sp. NGR234	J03686 NGRNODSU	-	
<i>nodU</i> (partially)	<i>Rhizobium</i> sp. NGR234	J03686 NGRNODSU	-	
<i>nodU</i> (full)	<i>Rhizobium</i> sp.*	X39965 RSNODUGEN	-	
<i>noIXWBTTIV</i>	<i>Rhizobium fredii</i> USDA 257#	L12231 RHMNOLBTU	-	<i>noIXWB</i> , <i>noIU</i>
ORF1; ORP2 (partially)	<i>Rhizobium</i> sp. NGR234	X74314 RSORF	+	NoIT: 97% identical (amino acid sequence level)
ORF140 nodulation gene;	<i>Rhizobium</i> sp. NGR234	X74068 RSPLAS	+	NoIX, NoIV+ORF4 of pNGR234a show significant differences to USDA257 (see table 2)
ORP91 (partially)				database entry includes sequencing mistakes causing frameshifts
RFXS9 25kDa-protein gene*	<i>Rhizobium fredii</i> USDA 257#	U18764 RFU18764	+	repetitive element in pNGR234a showing insertions, deletions of nucleotides in comparison to the database entry

* strains representing derivatives of NGR234: *Rhizobium* sp. ANU 240, *Rhizobium* sp. mpik 3030, *Rhizobium* sp.

strains closely related to NGR234: *Rhizobium fredii* USDA 257, *Rhizobium japonicum* USDA 191, *Rhizobium fredii* USDA 201.

* identity in nucleotide sequence as well as amino acid sequence

identified in Table 3 (except "ORF1") are reproduced in Table 4. Most of the 76 ORFs and their deduced proteins showed homologies to public database entries that could help identify their putative functions. Only ORFs L5 and L26 (duplicated *nifH*) as well as M16, M17 and M19 (*noIW*, *noIB* and *noIU*) were identical to database entries (98-100% homology). In the case of 7 ORFs and their deduced proteins, no homologous sequences in public databases have

been found.

As a second step, the remaining 436 kb of pNGR234a were analyzed using the methods noted above.

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(vi) CURRENT APPLICATION DATA:

(A) APPLICATION NUMBER: EP96730001.3
 (B) FILING DATE: 12th July 1996

(2) INFORMATION FOR SEQ ID NO:1:

(i) SEQUENCE CHARACTERISTICS:

(A) LENGTH: 536165 base pairs
 (B) TYPE: DNA
 (C) STRANDEDNESS: double
 (D) TOPOLOGY: linear

(ii) MOLECULE TYPE: DNA (genomic)

(iii) HYPOTHETICAL: No

(xi) SEQUENCE DESCRIPTION: SEQ ID NO:1:

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 CACGCTTGCG CTCATATCGA AGGGCCCGTC ATGCACCAGC GGCCAGCCGC CGTGCGCGCC 240
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	ACTATTCTGC	GCGGTTGCA	ATTCATGATC	TGCTCGGATT	CGGCAAAATG	CATCATCCGG	1980
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	TGCGCAAGTG	CAATGCCATC	CTCCTCGCTC	AAGCCGAACA	CACGCACCGA	CATCCTTCCC	2220
	ACGGCGCTGG	CGACACGGTC	GCAATAGAGA	TCCAGGGTTG	CCATTTTGGG	CGCGCGGATG	2280
	TCTTGTAGTA	CGTCCATTTC	CATGCCGTCG	ACAACGGGTA	GGAAATCCTC	TGCTTTCAGC	2340
	CCGAAGGTCG	TTACCGAGGC	GAGATGATCC	TTAGCCGCGC	GCGGCGGTAC	ACATTGGTAG	2400
	AGCGCGTCAA	TGTGATCGCG	CCATTGCTGA	AGTGCAGCAA	GGCGGTGCTC	GCGCGGTTCC	2460
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 GATGGTGTGG GAGGGAGCGG CGCCGTGGGG CGTCTTTGCA AACCGGTGTC AGTGCCAGAG 5160
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Claims

1. The nucleotide sequence as shown in Figure 3 or degenerate variants thereof.
- 5 2. The nucleotide sequence of claim 1 which has been altered by mutation, deletion or insertion.
3. ORFs derivable from the nucleotide sequence of claim 1 or claim 2; excluding the ORFs identified as L5, L26, M16, M17 and M19 in Table 4.
- 10 4. ORFs K1 to K23, L1 to L25 and M1 to M27 as identified in Table 4; excluding the ORFs identified as L5, L26, M16, M17 and M19 in Table 4.
5. The ORFs of claim 3 or claim 4 which encode the functions of:
 - 15 (a) nitrogen fixation,
 - (b) nodulation,
 - (c) transportation or encapsulation,
 - 20 (d) secretion (of proteins or other biomolecules),
 - (e) transcriptional regulation or DNA-binding,
 - 25 (f) peptidolysis or proteolysis,
 - (g) transposition or integration,
 - (h) rhizopine biosynthesis,
 - 30 or which encode:
 - (i) proteins exhibiting similarities to proteins of amino acid metabolism or related ORFs, or
 - (j) proteins putatively involved in the degradation of xenobiotic compounds.
- 35 6. The ORFs of any one of claims 3 to 5 which are under the control of their natural regulatory elements or under the control of analogues to such natural regulatory elements.
7. Intergenic sequences derivable from the nucleotide sequence of claim 1 or claim 2.
- 40 8. The intergenic sequences of claim 7 which are regulatory DNA sequences or repeated elements.
9. Proteins expressible from the nucleotide sequences or ORFs of any one of claims 1 to 6.
- 45 10. Use of the nucleotide sequences or ORFs of any one of claims 1 to 8 or the proteins of claim 9 in the analysis of the structure, organisation or dynamics of other genomes.
11. Use of the nucleotide sequences or ORFs of any one of claims 1 to 8 or the proteins of claim 9 in:
 - 50 (a) screening nucleotide sequences,
 - (b) subcloning nucleotide sequences,
 - (c) amplifying nucleotide sequences by PCR, or
 - 55 (d) gene trapping.
12. Use according to claim 11, wherein said nucleotide sequences are coding sequences or non-coding sequences.

13. Use according to claim 12, wherein said coding sequences are regulatory sequences or repeated elements.
14. Use according to any one of claims 10 to 13, wherein said nucleotide sequences or ORFs are oligonucleotide primers or hybridization probes.
15. Use of the nucleotide sequences, individual ORFs or groups of ORFs of any one of claims 1 to 8 or the proteins of claim 9 in:
- (a) the identification and classification of organisms and their genetic information,
 - (b) the identification and characterisation of nucleotide sequences, amino acid sequences or proteins,
 - (c) the transportation of compounds to and from an organism which is host to at least one of said nucleotide sequences, ORFs or proteins,
 - (d) the degradation and/or metabolism of organic, inorganic, natural or xenobiotic substances in a host organism, or
 - (e) the modification of the host-range, nitrogen fixation abilities, fitness or competitiveness of organisms.
16. The plasmid comprising the nucleotide sequence of claim 1 or claim 2.
17. A plasmid which harbours at least one ORF of any one of claims 1 to 8 or any degenerate variant thereof or which harbours at least one ORF or any degenerate variant thereof which encodes one or more of the proteins of claim 9.
18. The plasmid of claim 16 or claim 17 produced recombinantly.
19. The plasmid of any one of claims 16 to 18 or any variant thereof produced by mutation, deletion, insertion or inactivation of an ORF, ORFs or groups of ORFs.
20. Use of the plasmid of any one of claims 16 to 19 in:
- (a) obtaining a synthetic minimal set of ORFs required for functional *Rhizobium*-legume symbiosis,
 - (b) the modification of the host-range of rhizobia,
 - (c) the augmentation of the fitness or competitiveness of *Rhizobium* sp. NGR234 in the soil and its nodulation efficiency on host plants,
 - (d) the introduction of desired phenotype(s) into host plants using said plasmid as a stable shuttle system for foreign DNA encoding said desired phenotype(s), or
 - (e) the direct transfer of said plasmid into rhizobia or other microorganisms without using other vectors for mobilization.

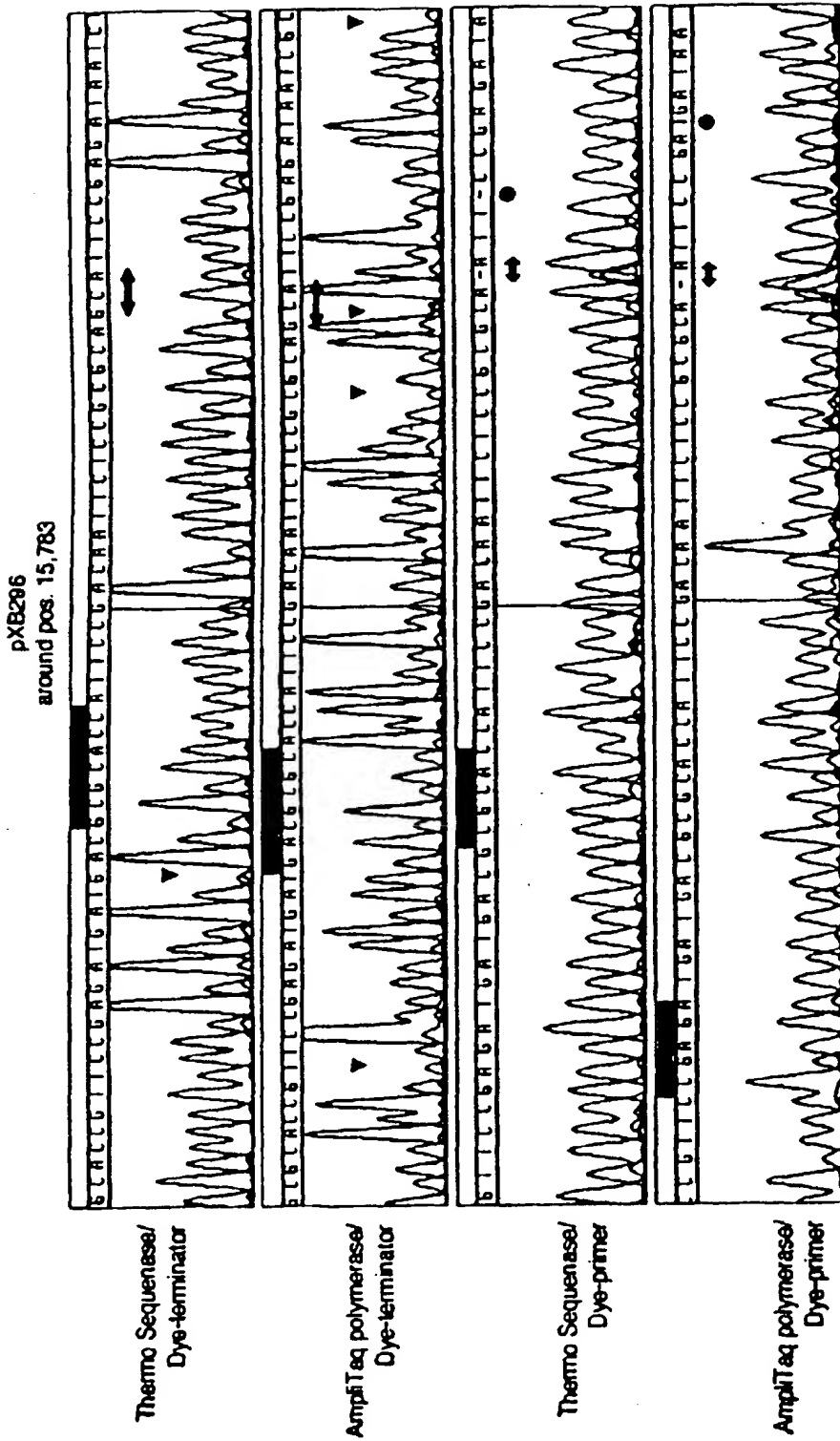


Figure 1. Comparison of sequences from pXB296 created by different cycle sequencing methods. The graphic outputs (program XGAP) of four electropherograms (traces) with the corresponding sequences generated by automatic base calling are shown around the pXB296 sequence position 15,783 (vertical line in the middle of each sequence). The readings cover a part of the minus strand of pXB296. (▼) Extremely low signals produced with dye terminators; (↔) the sequence GCA, which is compressed in dye primer scans; (●) automatic base-calling inaccuracies.

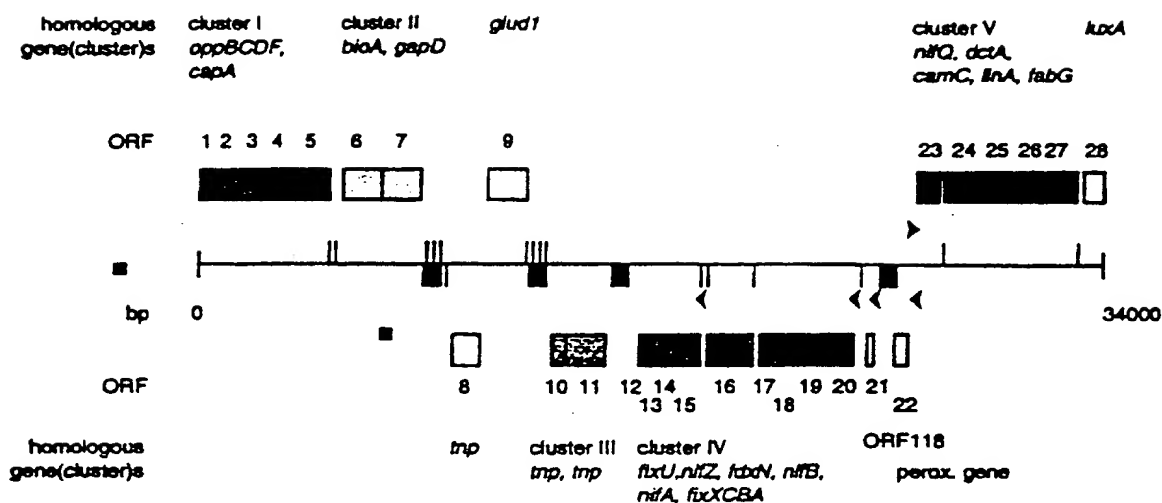


Figure 2. Organization of the predicted genes in pXB296 from *Rhizobium* sp. NGR234. Significant stem-loops (◡)/stem-loop clusters (■), which might function as ρ -independent transcription terminators, are represented. Sequence motifs (open arrowhead), similar to σ^{54} -dependent promoter consensus sequences (TGGCACG-N₄-TTGC) + *nifA* upstream activator sequences (TGT-N₁₀-ACA), are located at the following positions on the cosmid: 19,107–19,120 + 19,195–19,210; 24,787–24,800 + 24,878–24,893; 25,508–25,521 + 25,567–25,582; 26,815–26,828 + 26,941–26,956 (all minus strand); 27,074–27,131 (several possibilities) + 26,969–26,984 (plus strand).

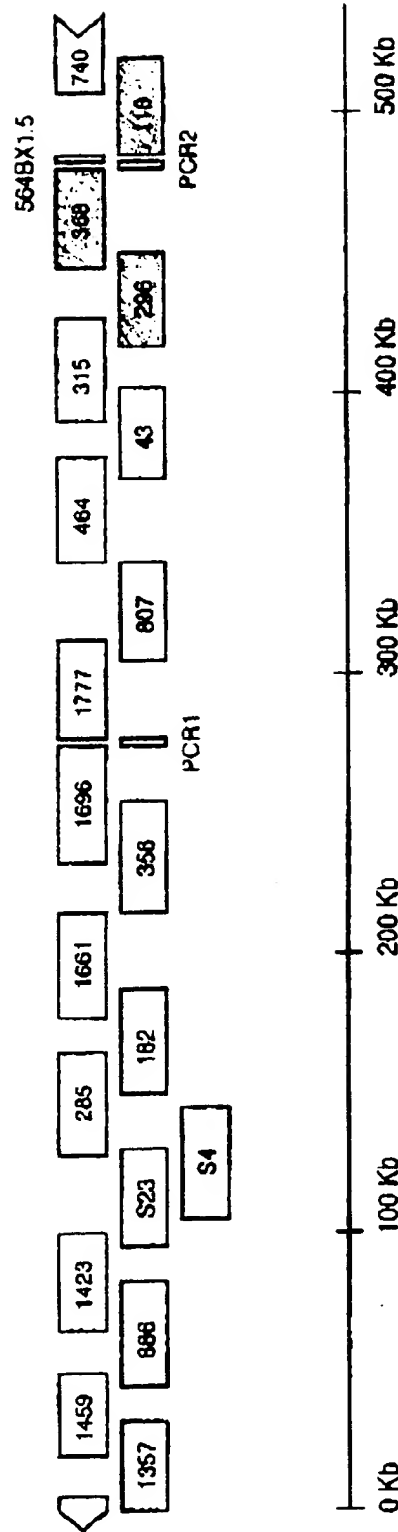


Figure 4: Map of the 20 sequenced cosmids covering the 536-Kb symbiotic plasmid of *Rhizobium* sp. NGR234.

The cosmid names consist of the prefix pXB and numbers that are given in the graphic.

PCR1: PCR product covering the gap between two cosmids from position 276,448 to 277,944.

564BX1.5 and PCR2: a subcloned 1.5-Kb DNA-fragment derived from cosmid pXB564 and a PCR product covering the gap between two cosmids from pos. 480,607 to 483,991.

Grey coloured areas cover the region from pos. 417,796 to 517,279 mentioned in the text.



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Application Number

which under Rule 45 of the European Patent Convention EP 96 73 0001 shall be considered, for the purposes of subsequent proceedings, as the European search report

DOCUMENTS CONSIDERED TO BE RELEVANT			
Category	Citation of document with indication, where appropriate, of relevant passages	Relevant to claim	CLASSIFICATION OF THE APPLICATION (Int.Cl.6)
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D,X	WO 94 00466 A (INST NAT RECH AGRONOMIQUE ;CENTRE NAT RECH SCIENT) 6 January 1994 * page 7, line 25 - page 8, line 11 * -/-	1-20	TECHNICAL FIELDS SEARCHED (Int.Cl.6) C07K C12N
INCOMPLETE SEARCH			
<p>The Search Division considers that the present European patent application does not comply with the provisions of the European Patent Convention to such an extent that it is not possible to carry out a meaningful search into the state of the art on the basis of some of the claims.</p> <p>Claims searched completely : 1,2,16-20</p> <p>Claims searched incompletely : 3-15</p> <p>Claims not searched :</p> <p>Reason for the limitation of the search:</p> <p>Claims 3-15 are not sufficiently disclosed and therefore were not specifically searched (Art. 83 and 84 EPC).</p>			
Place of search		Date of completion of the search	Examiner
BERLIN		4 August 1997	De Kok, A
<p>CATEGORY OF CITED DOCUMENTS</p> <p>X : particularly relevant if taken alone Y : particularly relevant if combined with another document of the same category A : technological background O : non-written disclosure P : intermediate document</p> <p>T : theory or principle underlying the invention E : earlier patent document, but published on, or after the filing date D : document cited in the application L : document cited for other reasons * : member of the same patent family, corresponding document</p>			

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EP 96 73 0001

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D,X	<p>MOLECULAR PLANT-MICROBE INTERACTIONS, vol. 5, no. 2, 1992, NEW YORK US, pages 179-186, XP002036798 J.C. VAN SLOOTEN ET AL.: "Two C4-dicarboxylate transport systems in Rhizobium sp. NGR234" * the whole document *</p> <p>---</p>	1-10	TECHNICAL FIELDS SEARCHED (Int.Cl.6)
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